Fitness consequences of dispersal

Ecology, 94(6), 2013, pp. 1287–1295

Fitness consequences of dispersal: Is leaving home the best of a bad lot?

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Abstract. Using 20 years of demographic and genetic data from four populations of banner-tailed kangaroo rats (*Dipodomys spectabilis*), we asked whether dispersing individuals gain benefits during adulthood that might compensate for the substantial survival costs they experience as juveniles. Compared to philopatric animals, within- and between-population dispersers gained no measureable advantages in adult survival, fecundity, or probability of recruiting offspring to adulthood. Restricting analyses to members of two central populations living more than 15 times the median dispersal distance from the study site edge, and using peripheral populations only to detect dispersal or offspring recruitment "offsite," did not change this result. Population density during year of birth had small negative effects on adult survival and fecundity, but there were no interactions with dispersal phenotype. We found no evidence that dispersers gained access to superior habitat or that their offspring suffered less inbreeding depression. Our results are consistent with fitness advantages being indirect; by leaving, dispersers release their kin from competition. Our results are also consistent with the possibility that dispersal is the "best of a bad lot." If dispersal is a conditional strategy, then the benefits may be obscured in observational data that compare dispersing individuals to philopatric individuals rather than to individuals whose dispersal phenotype is experimentally manipulated.

Key words: Dipodomys spectabilis; *dispersal; heteromyid rodent; inbreeding avoidance; kangaroo rat; kin competition; phenotypic polymorphism; philopatry; recruitment; reproductive success; survivorship.*

Introduction

Dispersal involves a phenotypic polymorphism: some individuals never leave home and others do. Considerable evidence supports the notion that dispersal has costs. Individuals moving through or attempting to settle in unfamiliar terrain risk increased predation, contact with novel pathogens, starvation, physical exposure, and/or aggression from conspecifics; during dispersal, individuals can also lose reproductive opportunities (Pusey and Packer 1987, Alberts and Altmann 1995, Bélichon et al. 1996, Doligez and Pärt 2008, Devillard and Bray 2009). Why do both dispersing and philopatric (nondispersing) phenotypes persist in the population, given that many dispersers perish in the attempt? Is dispersal, like some components of other phenotypic polymorphisms (Oliviera et al. 2008), simply "the best of a bad lot"?

A common view has been that mammalian dispersers incur costs during the "transience" and "settlement" phases of dispersal (Johnson and Gaines 1990, Larsen and Boutin 1994, Stamps 2001, Bonte et al. 2012), but gain compensatory advantages (relative to philopatric individuals) later in life. Two of the traditional "drivers" of dispersal—inbreeding avoidance and the opportunistic exploitation of ephemeral habitats—incorporate the expectation that dispersal increases survival and/or reproduction, but they differ in which generation these effects are manifest. If within- or between-population dispersers avoid inbreeding, they should give birth to viable young more often and/or recruit more offspring into the next generation than do philopatric individuals. On the other hand, increased survival and/or reproduction of between-population dispersers (relative to philopatric individuals and within-population dispersers) would suggest that they take advantage of spatiotemporal variation in habitat quality.

A rather different expectation, however, arose from an influential series of papers (Hamilton and May 1977, Comins et al. 1980) showing that a parental strategy that forces a proportion of offspring to disperse is evolutionarily stable even when dispersal is, in their words, an "almost-suicidal venture" (Hamilton and May 1977:578). In these models, dispersing and philopatric individuals are explicitly assumed to compete equally

Manuscript received 19 June 2012; revised 7 December 2012; accepted 2 January 2013. Corresponding Editor: T. J. Valone.
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after dispersal is completed; in other words, dispersers gain no reproductive or adult survival benefits to compensate for their early survival costs.

Observational evidence from mammals suggests that parental aggression is rarely required for dispersal of offspring (Wolff 1993, Smale et al. 1997), but Hamilton and May's basic result follows even when dispersal is under offspring control. If dispersing juveniles incur survival costs, selection on offspring will favor a lower dispersal propensity than selection on parents does. Nevertheless, dispersal should generally occur even if there is no compensatory increase in fecundity or survival later in life (Motro 1983, Starrfelt and Kokko 2010, Uller and Pen 2011). This can be understood in terms of kin selection: dispersers gain by reducing competition with relatives. By dispersing, individuals increase the fitness of the parents or siblings they leave behind: the indirect component of their own inclusive fitness (Taylor 1988, Lambin et al. 2001, Perrin and Goudet 2001).

Few studies have been able to produce lifetime data on survival and reproductive success of dispersers relative to philopatric individuals (reviewed by Bélichon et al. 1996, Doligez and Pärt 2008, Bonte et al. 2012). Here, we present such data for the banner-tailed kangaroo rat, *Dipodomys spectabilis*. This nocturnal, granivorous rodent larder-hoards and lives singly in large dirt mounds, making it easy to locate and retrap individuals throughout their lives (Skvarla et al. 2004). Breeding takes place primarily from December to March; by midsummer, the year's cohort is approaching adult size and both sexes have begun to disperse. The extent and timing of dispersal depends on population density: juveniles tend to disperse later during high-density years, and a higher proportion does not disperse at all (Jones et al. 1988). Most adults live near their birthplaces; the width of our study site (~2 km) is more than 50 times the median dispersal distance (Waser et al. 2006). Nearly all males and females breed first at age 1 year. Secondary dispersal is possible, but most individuals remain in the mound they inhabit at age 1 for the rest of their lives, which may last up to 6 years (Waser and Elliott 1991). Males and females have similar probabilities of dispersal, although female dispersers tend to settle slightly farther from their birth sites than do males (Busch et al. 2009).

Early studies of dispersal in banner-tailed kangaroo rats found that juveniles dispersing during their first summer had lower probabilities of surviving the following winter than did juveniles remaining in their natal mound. Jones (1986) reported that, conditional on surviving to October (when most dispersers have completed the process), philopatric juveniles were 1.7 times more likely than within-population dispersers to survive to the following March. Lower survival over their first winter is best viewed as a "settlement" cost experienced by dispersing juveniles. Additional survival costs associated with the "transience" phase of dispersal have been inferred from experiments in which natal mounds were fenced for ~5 days. Weaned juveniles were trapped within the enclosures and then released either inside or outside them. Juveniles forced to disperse in this way established themselves in new mounds within a month, but the proportion of philopatric controls that survived this period was 2.4 times greater than the proportion of surviving dispersers (Waser 1988). Transience and settlement costs together thus imply that philopatric juveniles are roughly four times as likely as within-population dispersers to survive their first year of life.

With genetic and demographic data collected during the more than 20 years since these early analyses, we can now ask whether the survival costs incurred by dispersing juveniles are counterbalanced by benefits that they acquire as adults. Because different postulated benefits of dispersal might act at different spatial scales (Fontanillas et al. 2004, Gauffre et al. 2009), we consider within- and between-population dispersers separately. We are unable to assess the indirect fitness benefits associated with dispersal, but we can estimate post-settlement effects, including adult survival, fecundity, recruitment, and the survival of offspring.

Because the consequences of dispersal often differ for males and females, and for animals born in surroundings with low vs. high population density (Smale et al. 1997, Matthysen 2005), we investigate the effects of both sex and density on adult survival, reproduction, and offspring recruitment. In addition, we investigate the possibility that estimates of the fitness of dispersers may be biased (Bélichon et al. 1996, Doligez and Pärt 2008) if they (or some of their offspring) disperse off the study site without being detected. Our hypotheses are listed in Table 1.

Methods

Kangaroo rats on our 2 × 3 km "Rucker" study site (31°37′ N, 109°15′ W; Cochise County, Arizona, USA) live in a set of eight spatially discrete clusters of mounds (Appendix A), linked by occasional dispersal, but largely independent demographically (Sanderlin et al. 2011). Our analyses are based on animals trapped during biannual censuses between 1990 and 2007 in four of these clusters (Waser and Hadfield 2011). One census each year was in March, near the end of the breeding season; the second was in July/August, when dispersal is underway. During each census, we used live-trapping records to determine each individual's residence (the mound that it lived in; Jones 1986). We used nine microsatellite markers to genotype all individuals. Field and genetic methodology are described in detail elsewhere (Jones 1986, Skvarla et al. 2004, Waser et al. 2006).

For each animal that survived to age 1, we assigned a dispersal phenotype. We considered its natal mound to be its first capture location or, where known, its mother's residence during the preceding breeding

season. If, during its first breeding season, it still resided in its natal mound, we considered it philopatric. If it lived in a different mound but within the same mound cluster, we scored it as a within-population disperser (median within-population dispersal distance = 34 m, range 5–267 m). If it lived in a different mound cluster, it was a between-population disperser (median between-population dispersal distance = 568 m, range 218–1082 m). Individuals first trapped as adults, and whose mother we could not determine, were scored as having an unknown dispersal phenotype.

Adult survival

Because some juveniles initiated dispersal after our August censuses, we could not reliably assign dispersal phenotypes before an individual reached adulthood. Therefore, we could not expand our early analyses of juvenile survival during the transience and settlement phases (Jones 1988, Waser 1988). Instead, we assessed whether or not adult survival rate differed between dispersal phenotypes, or whether survival of offspring was influenced by the dispersal phenotypes of their parents.

We used a model selection approach to investigate three sets of Cox proportional hazards survival models. First, we evaluated whether dispersal phenotype (along with sex and population density during the year of birth) influenced post-settlement survival. We modeled dispersal as a binary trait (dispersers vs. philopatric individuals). Jones (1988) found that the survival cost incurred by dispersing juveniles was density dependent: philopatric juveniles survived better than dispersers only at high population density. If adult survival were to show a similar pattern, the survival of dispersers and philopatric individuals might conceivably be equalized over the long term. To check this possibility, we included models with a density $\times$ dispersal phenotype interaction.

In a second analysis, we examined post-settlement survival with dispersal phenotype as a four-level categorical trait (within-population dispersers, between-population dispersers, philopatric individuals, and those of unknown dispersal phenotype). We also estimated life expectancy (conditional on surviving to age 1) for these four dispersal categories. Note that both the first and second analyses included only animals $\geq$1 year old, because dispersal phenotype is undetermined before age 1.

In a third analysis, we asked whether the dispersal phenotype of an individual's parents (either maternal or paternal), its sex, or population density in its year of birth influenced its survival beginning at first capture. In this analysis, we again modeled dispersal as a binary trait.

In all three analyses, we estimated population density each year as the number of animals trapped during the July/August census, and then categorized each year as either high density (above the mean) or low density (below the mean). To evaluate the models that best fit the data, we calculated Akaike's Information Criterion, corrected for small sample sizes (AIC_c), from the proportional hazards model.

Survival records were censored for individuals that were captured alive in the last census. Capture probabilities are high (median probability of capturing an adult at least once during a census = 0.98), and <1% of all animals move between populations as adults (Skvarla et al. 2004), so we assumed that any adult not captured during our last census had died.

To examine the possibility that we underestimated the survival of animals living near the study site edge because they later emigrated off the site, we repeated survival analyses for adults in the center of the study site. "Central" animals were those that reached adulthood in the central pair of our four populations, >600 m from any study site boundary; 600 m is more than 15 times the median dispersal distance, and fewer than 2% of kangaroo rats disperse this far during their lifetimes (Waser and Hadfield 2011). We conducted all survival analyses and tested their assumptions in SAS (PROC PHREG and PROC LIFETEST, SAS Institute, Cary, North Carolina, USA).

Fecundity

We compared the relative probabilities of reproduction (defined as producing an offspring that lived long enough to be trapped) among dispersal phenotypes. To do this, we used MasterBayes, a pedigree-estimation procedure that combines genetic, spatial, and demographic information in a Bayesian framework (Hadfield et al. 2006). MasterBayes simultaneously estimates parentage and population-level parameters of interest; here, the most important of these are the fecundities associated with dispersal phenotype. As demonstrated in earlier analyses (Hadfield et al. 2006, Koch et al. 2008, Walling et al. 2010), this approach efficiently uses the data from all individuals, even those whose parentage is not known with certainty, which increases power and reduces bias in parameter estimation. Note that "fecundity," as we define it, includes the effect of early juvenile mortality, because some juveniles inevitably die without being captured.

For the analyses reported here, we extended an earlier analysis (Waser and Hadfield 2011) that estimated the kangaroo rat pedigree, and fitted dispersal phenotype, population density in year of birth, and their interaction as predictors of overall fecundity. As in our survival analyses, dispersal phenotype was a categorical predictor with four levels: philopatry, within-population dispersal, between-population dispersal, and unknown. The effects of dispersal phenotype on paternity and maternity were allowed to differ, resulting in 14 parameters, with philopatric individuals set as the baseline category against which other dispersal strategies are compared. Data from all years were included in the analysis. We report MasterBayes' parameter estimates as odds ratios, including the 95% highest posterior density intervals.

TABLE 1. Summary of hypotheses and predictions for kangaroo rats (*Dipodomys spectabilis*) based on dispersal behavior.

Hypothesis	Expectations relative to philopatric animals	
	Adult survival	Fecundity
1) Dispersers avoid inbreeding as adults	equal in dispersers	higher in WP and BP dispersers
2) Dispersers find superior habitat patches	higher in BP dispersers	higher in BP dispersers
3) Dispersers avoid kin competition	no measureable difference	no measureable difference
4) Payoffs reverse with density	higher in dispersers at low density, lower at high density	
5) Dispersal is the "best of a bad lot"	equal or lower in dispersers	equal or lower in dispersers
6) Study site edge effects bias results	lower in dispersers near edge	

Notes: Dispersal is between populations (BP) or within population (WP). "Fecundity" includes survival from conception to first capture, and "recruitment" includes survival from conception to age 1 year. Where a cell is empty, no clear expectation is derived from the hypothesis. The kin competition hypothesis assumes that dispersers gain indirect fitness, which we could not estimate. For further explanation, see *Discussion*: *. . . so is dispersal "the best of a bad lot"?*

We ran the MasterBayes model for 600 000 iterations, with a burn-in of 100 000 iterations and a thinning interval of 250. Flat improper priors were used for all parameters, and an approximation was used to account for the possibility of missing genotypes and phenotypes (Koch et al. 2008). Both the allelic dropout rate and the stochastic error rate were set to 0.01, following an analysis in which the rates were estimated from repeat samples. Statistical issues related to these analyses are described in more detail in Waser and Hadfield (2011), and we present the relevant MasterBayes code as a Supplement. In Appendix D, we also present the results of a parallel analysis treating dispersal distance as a continuous variable.

A complication with our analyses is that individuals' dispersal phenotypes can often be updated using the genetic data if the natal mound of an individual can be inferred by identifying its mother. Ideally the pedigree, dispersal phenotype, and the effect of dispersal phenotype on fecundity would be estimated in a single analysis, but MasterBayes requires that predictors of fecundity (such as dispersal phenotype) are known a priori. As a compromise, we used the data from our initial MasterBayes run (Waser and Hadfield 2011) to update dispersal phenotypes. This analysis indicated that some individuals initially classified as philopatric (based on trapping data alone) were in fact dispersers (based on the location of the mothers they were assigned to with 95% certainty), having left their mother's mound prior to first capture. In addition, we were able to resolve the phenotype of many animals whose dispersal status was initially unknown because we had not trapped them before they reached adulthood. Results that we report here are based on these updated phenotype assignments.

Recruitment

We could not estimate lifetime reproductive success (including the combined effects of juvenile survival, adult survival, and fecundity on lifetime zygote production), because we could not define an individual's dispersal phenotype until it had reached adulthood. Instead, we used the usual onset of adulthood as a starting point, and compared the success of different dispersal phenotypes in producing offspring that survived to age 1. To do this, we performed a MasterBayes analysis of recruitment, parallel to the analysis of fecundity, but based only on the subset of offspring that survived to age 1 or beyond.

Finally, we checked whether our estimates of recruitment for animals living near the edge of the study site were negatively biased because some of their offspring disperse and reach maturity undetected off the study site (Doligez and Pärt 2008). To do this, we ran the recruitment model with seven dispersal phenotypes for each sex rather than four: philopatric animals of central origin, philopatric animals of peripheral origin, within-population dispersers of central origin, within-population dispersers of peripheral origin, between-population dispersers of central origin, between-population dispersers of peripheral origin, and individuals of unknown dispersal status. To limit the number of parameters in the model, this last analysis ignored density and its interactions with dispersal phenotype.

RESULTS

We used 1755 animals born on the study site during the study for pedigree reconstruction; 720 of these (355 females, 365 males) survived to reproductive maturity at age 1 and thus formed the basis of our comparisons of dispersal phenotypes. Of these 720, 190 (26%) were classified as philopatric, 337 (47%) as within-population dispersers, and 37 (5%) as between-population dispersers. The remaining 156 (22%) had unknown dispersal phenotypes. Of the 720, 247 (34%) were from the study site center.

Adult survival

In all models evaluated, tests of proportional hazards indicated that the hazard ratio remained the same across ages, thus satisfying model assumptions. In the first set of models, which evaluate the contribution of dispersal phenotype, density, and sex on post-settlement survival, no model performed significantly better than the null

TABLE 1. Extended.

Expectations relative to philopatric animals		
Recruitment	Offspring survival	Comments
higher in WP and BP dispersers	higher in offspring of WP and BP dispersers	effects possibly greater at high density
possibly higher in BP dispersers	possibly higher in BP dispersers	
no measureable difference	no measureable difference	fitness benefits indirect suggested by Jones (1988)
equal or lower in dispersers	equal or lower in offspring of dispersers	
lower in dispersers near edge	lower in dispersers near edge	

(Table 2). The lowest-AIC_c model included density, but no model containing dispersal phenotype or its interaction with density performed better than the null, and no models were statistically significant. Thus we found no evidence that dispersers survived better than philopatric animals. Focusing on animals from the central portion of the study site gave similar results; none of the independent variables were significant predictors of adult survival.

The second set of models, which treated within- and between-population dispersers separately and also included individuals of unknown dispersal phenotype, gave similar results. The null model had the lowest AIC_c, and no models incorporating dispersal phenotype performed significantly better than the null (Appendix B). Estimated life expectancies at age 1 were 2.3 ± 0.1 years (mean ± SE) for philopatric individuals, 2.2 ± 0.1 years for within-population dispersers, 1.9 ± 0.2 years for between-population dispersers, and 2.2 ± 0.1 years for animals of unknown dispersal phenotype. Survivorship curves were virtually independent of phenotype (Fig. 1).

In the third set of models, which evaluate whether parental dispersal phenotype, density, and sex contribute significantly to differences in survival from age at first capture, AIC_c values suggest that a model that includes density in the year of birth and mother's dispersal phenotype best fit the data (Appendix C; $n = 474$, $LR = 11.31$, $df = 2$, $P = 0.004$). However, although P is highly significant for the density term in the model ($P = 0.002$), the P value for mother's dispersal phenotype is marginal ($P = 0.07$). Comparing the model that contains both of these terms to one that includes only density shows that adding maternal dispersal phenotype does not significantly improve the model ($LR = 3.19$, $df = 1$, $P = 0.07$). We therefore interpret the parameter estimate from the density-only model ($n = 474$, $LR = 8.12$, $df = 1$, $P = 0.004$) when evaluating survivorship of individuals from first capture on. In this model, the hazard ratio was 0.73, indicating that individuals born in years of high population density suffer approximately a 37% decrease in annual survival relative to those born in low-density years.

To further assess any possible impact of maternal dispersal tendency on offspring survival, we examined offspring survival between first capture and age 1 (when effects of parental dispersal phenotype would presumably be strongest). We found that 70 of 307 offspring of dispersing mothers survived to age 1 (23%), compared to 23 of 137 offspring of philopatric mothers (17% ; $P = 0.17$, Fisher exact test).

Fecundity

We observed no significant effects of dispersal phenotype on a female's probability of producing an offspring. Neither within- nor between-population dispersal produced any apparent reproductive advantage. Results for females of unknown dispersal phenotype were intermediate between those for within- and between-population dispersers (Table 3). A parallel analysis in which we treated dispersal distance as a continuous variable gave the same result (Appendix D).

Density during the year of birth had no detectable effect on the ability of a female to produce offspring when she reached maturity (but see Appendix D), nor did we see any evidence for an interaction between density and (female) dispersal phenotype.

Results were similar for males. Dispersal phenotype did not significantly affect fecundity. Males born in years of high population density were very slightly, but significantly less likely to produce offspring, but there were no significant interactions between density and dispersal phenotype (Table 3).

Recruitment

We found no evidence that dispersal phenotype influenced the ability of either males or females to recruit offspring into the breeding population. Indeed, restricting the MasterBayes analysis to recruits, rather than all offspring, had practically no effect on the results (Table 3). Density during the year of birth had a very slight negative effect on males, but not females, and interactions were not significant. Odds ratios in the "fecundity" and "recruitment" columns of Table 3 are virtually identical.

Considering central and peripheral animals separately, we found no significant effects of centrality (Appendix E). Nevertheless, we remained concerned that we might be missing recruits that dispersed off the study

TABLE 2. Model comparisons for kangaroo rat survival beginning at age 1, evaluating effects of dispersal phenotype (DP), population density in the year of birth, sex, and interactions between DP and density.

Independent variables	−2 log L	AIC_c	ΔAIC	LR	*P*(LR)
Density	4946.21	4948.25	0.00	2.13	0.14
[null model]	4948.34	4948.36	0.11		
DP, density	4944.71	4948.78	0.53	3.63	0.16
DP	4946.74	4948.78	0.53	1.60	0.21
Sex	4946.86	4948.90	0.65	1.48	0.22
Density, sex	4944.87	4948.94	0.69	3.47	0.18
DP, sex	4945.30	4949.37	1.11	3.04	0.22
DP, density, sex	4943.40	4949.50	1.25	4.94	0.18
DP × density	4947.94	4949.98	1.72	0.40	0.53
DP × density, DP, density, sex	4942.44	4950.59	2.33	5.90	0.21

Notes: Dispersal phenotype (DP) is modeled as a binary trait: dispersers and philopatric individuals. Log-likelihood (−2 log L) and Akaike Information Criterion (corrected for small sample sizes, AIC_c) values are given, as well as LR, the likelihood ratio of the relevant model to the null model (with no independent variables); *P*(LR) is the associated *P* value; $N = 593$ is the total number of adults of known dispersal phenotype.

site, especially from peripheral between-population dispersers, for which our sample sizes were small. To check whether such an edge effect influenced our results, we examined recruitment estimates from centrally born animals only (Table 4). As in our initial analyses, we detected no effect of dispersal phenotype on the probability of recruiting yearlings for either females or males.

DISCUSSION

Our data support two emerging generalizations about mammalian dispersal. First, the costs of dispersal were restricted to its transience and settlement phases. But second, we detected no direct fitness benefits that would compensate for those costs, in particular those expected from inbreeding avoidance or from moving to high-quality habitat patches. Once dispersal was completed, adults of different dispersal phenotypes fared equally well in survival and reproduction.

Costs of dispersal are short term . . .

Our previously published data (Jones 1988, Waser 1988) indicated that dispersal increases the mortality of juveniles roughly fourfold, but the data reported here revealed no negative effects of dispersal on survival after settlement occurs. Moreover, dispersal did not measurably degrade an individual's subsequent ability to produce offspring.

Even with data from 1755 animals in 17 successive cohorts, we cannot be sure that post-settlement costs are truly nonexistent. For example, because few animals dispersed between populations, confidence intervals for their survival and fecundity estimates are relatively broad. But the lower bounds of these estimates imply fitness penalties that are small relative to the survival cost experienced by juveniles. Our results are thus consistent with the generalization that dispersal costs are primarily associated with the processes of movement and/or settlement (Soulsbury et al. 2008, Devillard and Bray 2009, Bonte et al. 2012).

. . . but dispersers gain nothing in adult survival or fecundity

Although we found no evidence that adults paid fitness costs for dispersing, we also found no evidence of compensatory benefits. Results were the same if we treated dispersal distance as a continuous variable (Appendix D), whether based on our complete sample of 720 adults or only on animals that live far from possible edge effects. For example, the odds that a dispersing animal recruits an offspring (relative to one that is philopatric) range from 0.83 to 1.25, depending on sex and dispersal phenotype when estimated with the complete data set, and from 0.96 to 1.19 when estimated from central animals alone.

If there were differences among populations in habitat quality and dispersers tended to move to superior

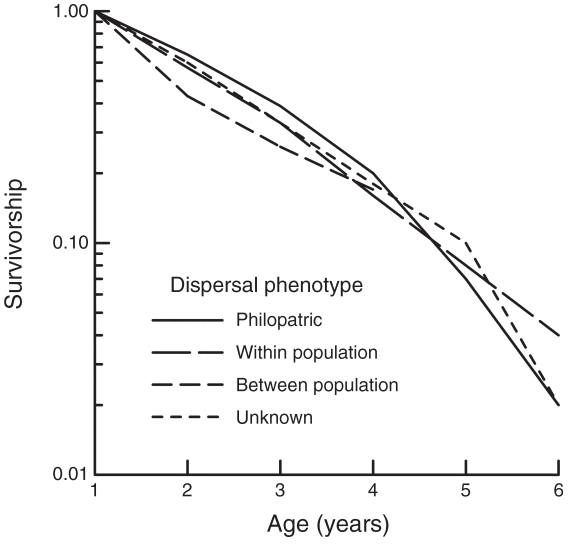

FIG. 1. Survivorship of adult kangaroo rats (*Dipodomys spectabilis*) as a function of dispersal phenotype. No significant differences were observed (Wilcoxon $\chi^2 = 4.14$, df = 3, $P = 0.25$; PROC LIFETEST). The sample size for between-population dispersers is too low to estimate survivorship past age 3.

TABLE 3. Parameters relating kangaroo rat fecundity to sex, dispersal phenotype, population density, and the density–dispersal interaction.

Phenotype and density, by sex	Fecundity		Recruitment	
	Posterior mean	95% HPD interval	Posterior mean	95% HPD interval
A) Female				
Dispersal phenotype				
Within population	1.193	0.930 to 1.507	1.245	0.975 to 1.564
Between population	0.747	0.409 to 1.424	0.833	0.445 to 1.558
Unknown	0.957	0.751 to 1.219	1.061	0.809 to 1.391
Density	1.000	0.996 to 1.000	0.999	0.996 to 1.003
Density × dispersal				
Within population	0.998	0.996 to 1.002	0.999	0.996 to 1.003
Between population	0.993	0.985 to 1.000	0.993	0.986 to 1.000
Unknown	0.997	0.994 to 1.001	0.997	0.993 to 1.001
B) Male				
Dispersal phenotype				
Within population	1.011	0.811 to 1.124	0.960	0.778 to 1.195
Between population	1.008	0.610 to 1.596	1.051	0.679 to 1.670
Unknown	1.086	0.849 to 1.373	1.178	0.923 to 1.517
Density	**0.996**	**0.994 to 0.999**	**0.996**	**0.994 to 0.999**
Density × dispersal				
Within population	1.000	0.997 to 1.003	1.000	0.997 to 1.003
Between population	0.996	0.990 to 1.003	0.997	0.992 to 1.004
Unknown	1.001	0.998 to 1.004	1.001	0.998 to 1.004

Notes: Parameters are presented as the odds ratio that an individual of the designated dispersal phenotype produces an offspring that survives to independence (fecundity) or to age 1 (recruitment) relative to the odds that a philopatric adult does so. Parameters in boldface are those with a 95% highest posterior density (HPD) interval that does not overlap 1.0.

patches, long-distance dispersal should have increased life span or fecundity. However, the post-dispersal life expectancy of between-population dispersers (2.0 years) was not greater than that of philopatric animals (2.3 years), and between-population dispersers were no more likely than philopatric individuals to produce offspring (odds ratio 0.75 and 1.01 for females and males, respectively).

Similarly, we found no evidence that dispersal reduced inbreeding depression. Neither within- nor between-population dispersers suffered lower fecundity or recruitment than animals that did not disperse. Moreover, the offspring of dispersers survived just as well as those whose parents were philopatric.

The apparent absence of direct fitness advantages is not an artifact of study site edge effects, which appear to be small based on the comparison of the full data set with that confined to central animals. Simulations by Doligez and Pärt (2008) have shown that edge effects should be small when the study site is very large relative to median dispersal distances, when secondary dispersal is rare, and when parent and offspring dispersal phenotypes are poorly correlated, all conditions that were met in this study.

Jones (1988) reported that the negative effect of dispersal on juvenile survival was modulated by population density; philopatric kangaroo rats survived their first winter 2.2 times as well as within-population dispersers during years of high population density, but only 0.8 times as well during low-density years. We found no such density dependence in adult survival or fecundity. Adults born when population density was high later survived and reproduced less well than those born when density was low, but density effects were extremely small and were independent of dispersal phenotype. Adult survival and fecundity did not "compensate" for lower survival during dispersal at any density.

. . .so is dispersal "the best of a bad lot"?

In sum, our data are remarkably concordant with the simplified assumption made by Hamilton and May

TABLE 4. Parameters relating yearling recruitment to sex and dispersal phenotype, for adult kangaroo rats originating in central populations only.

Dispersal phenotype, by sex	Recruitment	
	Posterior mean	95% HPD interval
Female		
Within population	1.06	0.71 to 1.59
Between population	0.98	0.57 to 1.79
Unknown	0.96	0.60 to 1.43
Male		
Within population	0.97	0.74 to 1.33
Between population	1.19	0.67 to 1.79
Unknown	1.11	0.79 to 1.62

Notes: Parameters are presented as the odds ratio that an individual of the designated dispersal phenotype produces an offspring that survives to age 1, relative to the odds that a philopatric adult does so. In all cases, the 95% highest posterior density (HPD) interval overlaps 1.0.

(1977) that dispersers die during the process but, once settled in a new site, compete equally with adults that did not disperse. If dispersers gain direct fitness through inbreeding avoidance or access to superior habitat, those benefits are small compared to the survival costs suffered during transience and settlement.

This result leaves avoidance of kin competition as the most likely "driver" of dispersal. Evidence for the role of kin competition is difficult to obtain (Lambin et al. 2001, Cote and Clobert 2010), but results like ours are not unique. Of field studies that compare post-settlement survival and reproduction of dispersers and philopatric individuals, few report that dispersers do better (Bélichon et al. 1996, Doligez and Pärt 2008, Soulsbury et al. 2008).

Our data are also consistent with the possibility that dispersal is a conditional strategy (Ims and Hjermann 2001). In this view, dispersal would be undertaken only by individuals that, for some environmental or genetic reason, could not choose the better option of staying home. Dispersers would not have to survive and reproduce as well as philopatric individuals, but only better than they would have had they not dispersed. Young kangaroo rats inherit the natal mound when their mother dies or abdicates (Jones et al. 1988), but disperse otherwise; an early investigation of parent–offspring correlation in dispersal distance (Waser and Jones 1989) concluded that dispersal was probably conditional, perhaps related to the appearance of vacancies among nearby mounds.

When this study began more than two decades ago, the senior author imagined dispersal and philopatry as two "pure" strategies, the expectation being that we would observe a mixture of the two phenotypes at whatever frequencies equalized lifetime fitness. Our results do not support this view. Comparisons of offspring survival as a function of parental phenotype also show this view to be simplistic. If dispersing adults had dispersing offspring, then those offspring would suffer the fourfold survival costs associated with transience and settlement, and dispersers would be less likely than philopatric adults to recruit offspring into the next generation. Our data show no such effect, a result that is easy to understand if dispersing adults produce a mixture of dispersing and philopatric offspring. In other words, what evolves is a "dispersal propensity" (Hamilton and May 1977, Doncaster et al. 1997, Perrin and Goudet 2001), or, if dispersal is conditional, the reaction norm that specifies the threshold conditions that provoke emigration (Cote and Clobert 2010). Our results suggest the need for studies that manipulate dispersal "phenotype" experimentally. Moreover, the most appropriate question for future studies of the "drivers" of dispersal may not be about the fitness of individual dispersers (or nondispersers), but about the fitness consequences these decisions have for an individual's kin, and how these may be influenced by the familial similarity in dispersal tendency found by quantitative geneticists (Pasinelli et al. 2004).

Acknowledgments

We received support from the National Science Foundation (DEB-0816925). We thank N. Emery, A. Fahey, M. Hale, R. Howard, J. Lucas, and N. Marra for helpful comments, and A. DeWoody, J. Winters, B. Swanson, B. Keane, and J. Busch for discussion, microsatellite analyses, and help in the field. A. Edelman and J. Clobert provided extensive and helpful comments during manuscript review.

Literature Cited

Alberts, S. C., and J. Altmann. 1995. Balancing costs and opportunities: dispersal in male baboons. American Naturalist 145:279–306.

Bélichon, S., J. Clobert, and M. Massot. 1996. Are there differences in fitness components between philopatric and dispersing individuals? Acta Oecologia 16:503–517.

Bonte, D., et al. 2012. Costs of dispersal. Biological Reviews 87: 290–312.

Busch, J. D., P. M. Waser, and J. A. DeWoody. 2009. The influence of density and sex on patterns of fine-scale genetic structure. Evolution 63:2302–2314.

Comins, H. N., W. D. Hamilton, and R. M. May. 1980. Evolutionarily stable dispersal strategies. Journal of Theoretical Biology 82:205–230.

Cote, J., and J. Clobert. 2010. Risky dispersal: avoiding kin competition despite uncertainty. Ecology 91:1485–1493.

Devillard, S., and Y. Bray. 2009. Assessing the effect on survival of natal dispersal using multistate capture–recapture models. Ecology 90:2902–2912.

Doligez, B., and T. Pärt. 2008. Estimating fitness consequences of dispersal: a road to "know-where"? Non-random dispersal and the underestimation of dispersers' fitness. Journal of Animal Ecology 77:1199–1211.

Doncaster, C. P., J. Clobert, B. Doligez, E. Danchin, and L. Gustaffson. 1997. Balanced dispersal between spatially varying local populations: an alternative to the source–sink model. American Naturalist 150:425–445.

Fontanillas, P., E. Petit, and N. Perrin. 2004. Estimating sex-specific dispersal rates with autosomal markers in hierarchically-structured populations. Evolution 58:886–894.

Gauffre, B., E. Petit, S. Braudier, V. Bretagnolle, and J. F. Cosson. 2009. Sex-biased dispersal pattern depends on the spatial scale in a social rodent. Proceedings of the Royal Society B 276:3487–3494.

Hadfield, J. D., D. S. Richardson, and T. Burke. 2006. Towards unbiased parentage assignment: combining genetic, behavioural and spatial data in a Bayesian framework. Molecular Ecology 15:3715–3730.

Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. Nature 269:578–581.

Ims, R. O., and D. Ø. Hjermann. 2001. Condition-dependent dispersal. Pages 203–216 *in* J. Clobert, E. Danchin, A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, New York, New York, USA.

Johnson, M., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics 21: 449–480.

Jones, W. T. 1986. Survivorship in philopatric and dispersing kangaroo rats (*Dipodomys spectabilis*). Ecology 67:202–207.

Jones, W. T. 1988. Density-related changes in survival of philopatric and dispersing kangaroo rats. Ecology 69:1474–1478.

Jones, W. T., P. M. Waser, L. F. Elliott, N. E. Link, and B. B. Bush. 1988. Philopatry, dispersal, and habitat saturation in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. Ecology 69:1466–1479.

Koch, M., J. D. Hadfield, K. M. Sekc, and C. Sturmbauer. 2008. Pedigree reconstruction in wild cichlid fish populations. Molecular Ecology 17:4500–4511.
Lambin, X., J. Aars, and S. B. Piertney. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. Pages 110–122 *in* J. Clobert, E. Danchin, A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, New York, New York, USA.
Larsen, K. W., and S. Boutin. 1994. Movement, survival and settlement of red squirrels *Tamiasciurus hudsonicus*. Ecology 75:214–223.
Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.
Motro, U. 1983. Optimal rates of dispersal: parent–offspring conflict. Theoretical Population Biology 21:394–411.
Oliviera, R. F., M. Taborsky, and H. J. Brockmann, editors. 2008. Alternative reproductive tactics. Cambridge University Press, Cambridge, UK.
Pasinelli, G., K. Schiegg, and J. R. Walters. 2004. Genetic and environmental influences on natal dispersal distance in a resident bird species. American Naturalist 164:660–669.
Perrin, N., and J. Goudet. 2001. Inbreeding, kinship and the evolution of natal dispersal. Pages 123–142 *in* J. Clobert, E. Danchin, A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, New York, New York, USA.
Pusey, A. E., and C. Packer. 1987. The evolution of sex-biased dispersal in lions. Behaviour 101:275–310.
Sanderlin, J. S., P. M. Waser, J. E. Hines, and J. D. Nichols. 2011. On valuing patches: estimating contributions to metapopulation growth with reverse-time capture–recapture modeling. Proceedings of the Royal Society B 279:480–488.
Skvarla, J. L., J. D. Nichols, J. E. Hines, and P. M. Waser. 2004. Modeling interpopulation dispersal by banner-tailed kangaroo rats. Ecology 85:2737–2746.
Smale, L., S. Nunes, and K. E. Holekamp. 1997. Sexually dimorphic dispersal in mammals: patterns, causes and consequences. Advances in the Study of Behavior 26:181–251.
Soulsbury, C. D., P. J. Baker, G. Iossa, and S. Harris. 2008. Fitness costs of dispersal in red foxes (*Vulpes vulpes*). Behavioral Ecology and Sociobiology 62:1289–1298.
Stamps, J. A. 2001. Habitat selection by dispersers. Pages 230–242 *in* J. Clobert, E. Danchin, A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, New York, New York, USA.
Starrfelt, J., and H. Kokko. 2010. Parent–offspring conflict and the evolution of dispersal distance. American Naturalist 175: 38–49.
Taylor, P. D. 1988. An inclusive fitness model for dispersal of offspring. Journal of Theoretical Biology 130:363–378.
Uller, T., and I. Pen. 2011. A theoretical model of the evolution of maternal effects under parent–offspring conflict. Evolution 65:2075–2084.
Walling, C. A., J. M. Pemberton, J. D. Hadfield, and L. E. B. Kruuk. 2010. Comparing parentage inference software: reanalysis of a red deer pedigree. Molecular Ecology 19: 1914–1928.
Waser, P. M. 1988. Resources, philopatry, and social interactions among mammals. Pages 109–130 *in* C. N. Slobodchikoff, editor. Ecology of social behavior. Academic Press, New York, New York, USA.
Waser, P. M., J. Busch, C. R. McCormick, and J. A. DeWoody. 2006. Parentage analysis detects cryptic pre-capture dispersal in a philopatric rodent. Molecular Ecology 15:1929–1937.
Waser, P. M., and L. F. Elliott. 1991. Dispersal and genetic structure in kangaroo rats. Evolution 45:935–943.
Waser, P. M., and J. D. Hadfield. 2011. How much can parentage assignment tell us about interpopulation movement? Molecular Ecology 20:1277–1288.
Waser, P. M., and W. T. Jones. 1989. Heritability of dispersal in banner-tailed kangaroo rats, *Dipodomys spectabilis*. Animal Behaviour 37:987–991.
Wolff, J. O. 1993. What is the role of adults in mammalian juvenile dispersal? Oikos 68:173–176.

Supplemental Material

Appendix A

A map of the study site (*Ecological Archives* E094-114-A1).

Appendix B

A table summarizing model selection results relating adult survival to sex, density, and dispersal phenotype (*Ecological Archives* E094-114-A2).

Appendix C

A table summarizing model selection results relating offspring survival to sex, density, and parental dispersal phenotype (*Ecological Archives* E094-114-A3).

Appendix D

A table summarizing odds ratios of fecundity from a parallel MasterBayes analysis with dispersal distance fitted as a continuous variable (*Ecological Archives* E094-114-A4).

Appendix E

A table comparing the impact of dispersal phenotype on yearling recruitment from animals of central vs. peripheral origin (*Ecological Archives* E094-114-A5).

Supplement

R code used with MasterBayes to analyze the impact of dispersal phenotype and centrality on fecundity and recruitment (*Ecological Archives* E094-114-S1).